PB83-209809

Tidal and Diurnal Spawning Cues in the Atlantic Silverside, 'Menidia menidia'

(U.S.) Environmental Research Lab.
Gulf Breeze, FL

1983

U.S. Department of Commerce
National Technical Information Service
NTIS

TECHNICAL REPORT DATA
(Please read Instructions on the reverse before comple

1. REPORT NO. EPA-600/J-82-015	2. JOURNAL ARTICLE	3 PB83-209809
4. TITLE AND SUBTITLE Tidal and Diurnal Spawning Cues in the Atlantic Silverside, Menidia menidia		5. REPORT DATE 1983 6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) Douglas P. Middaugh and Toru Takita		8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS		10. PROGRAM ELEMENT NO. ACBE1A 11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS U.S. Environmental Protection Agency Office of Research and Development Environmental Research Laboratory Gulf Breeze, Florida 32561		13. TYPE OF REPORT AND PERIOD COVERED 14. SPONSORING AGENCY CODE EPA-600/04

15. SUPPLEMENTARY NOTES Env. Biol. Fish., 8(2):97-104, 1983

16. ABSTRACT Field and laboratory observations revealed tidal and diurnal cues for spawning in the Atlantic silverside, Menidia menidia. In the field, spawning runs began near the time of daytime high tides at flood tide velocities ranging from 3 to 16, $\bar{x}$ 11 cm sec^{-1}. Spawning runs ended at ebb tide velocities ranging from 5 to 22, $\bar{x}$ 17 cm sec^{-1}.

In the laboratory M. menidia were reared from embryos to sexual maturity in 10 months (April 1979 to January 1980). During this time, approximately 50 fish were held in each of two, 1 m diameter tanks. A pump was used to maintain a constant current velocity of 8 cm sec^{-1} in the holding tanks. Water temperature ranged from 16 to 25°C, the salinity was 30 ± 2 °/oo. Fish were fed Tetra-min flake food and Artemia nauplii each day. During January 1980, the seawater circulation pump was turned off twic daily for one hour, 1200 to 1300 and 2400 to 0100. Current velocities decreaded from 8 cm sec^{-1} to 0.0 cm sec^{-1} during these periods. M. menidia held under a 24 h light: 0 h dark (24L:0D) photoperoid spawned from 1200 to 1300 and 2400 to 0100 in response to decreased current velocities. Modification of the photoperiod to 14L:10D (with the circulating pump turned off from 1200 to 1300 and 2400 and 0100) resulted in spawning between 0500 and 0600 in response to "lights-on" and at 1200 to 1300 in response to decreased current velocities. No spawning occurred when current velocities decreased to 0.0 cm sec^{-1} between 2400 and 0100 during darkness.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

REPRODUCED BY
NATIONAL TECHNICAL
INFORMATION SERVICE
U.S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

18. DISTRIBUTION STATEMENT Release to public	19. SECURITY CLASS *(This Report)* Unclassified	21. NO. OF PAGES 9
	20. SECURITY CLASS *(This page)* Unclassified	22. PRICE

EPA-600/J-82-015
JOURNAL ARTICLE

Env. Biol. Fish. Vol. 8, No. 2, pp. 97-104, 1983

Tidal and diurnal spawning cues in the atlantic silverside, *Menidia menidia**

Douglas P. Middaugh[1] & Toru Takita[2]
[1] *U.S. Environmental Protection Agency, Gulf Breeze, Environmental Research Laboratory, Sabine Island, Gulf Breeze, Florida 32561, U.S.A.*
[2] *Faculty of Fisheries, Nagasaki University, 1-14 Bunyko Machi, Nagasaki 852, Japan*

Keywords:
Fish, Tidal currents, Diurnal cycle, Intertidal zone, Egg viability

Synopsis

Field and laboratory observations revealed tidal and diurnal cues for spawning in the atlantic silverside, *Menidia menidia*. In the field, spawning runs began approximately when daytime flood tide velocities ranged from 3 to 16 ($\bar{x} = 11$) cm sec^{-1}. Spawning runs ended at ebb tide velocities ranging from 5 to 22 ($\bar{x} = 17$) cm sec^{-1}.

In the laboratory, *M. menidia* were reared from embryos to sexual maturity in 10 months (April 1979 to January 1980). During this time approximately 50 fish were held in each of two, 1 m diameter tanks. A pump was used to maintain a constant current velocity of 8 cm sec^{-1} in the holding tanks. Water temperature ranged from 16 to 25° C, the salinity was 30 ± 2 ‰. Fish were fed Tetramin® flake food and *Artemia* nauplii each day. During January and February 1980, the seawater circulation pump was turned off twice daily for one hour, from 1200 to 1300 and 2400 to 0100. Current velocities decreased from 8.0 cm sec^{-1} to 0.0 cm sec^{-1} during these periods. *M. menidia* held under a 24 h light:0 h dark (24 L:0 D) photoperiod spawned from 1200 to 1300 and 2400 to 0100 in response to decreased current velocities. Modification of the photoperiod to 14 L:10 D (with the circulating pump turned off from 1200 to 1300 and 2400 to 0100) resulted in spawning between 0500 and 0600 in response to 'lights-on' and between 1200 and 1300 in response to decreased current velocities. No spawning occurred in response to the decreased current velocities during darkness.

The importance of timing of spawning runs to coincide with low current velocities was revealed in tests to determine the duration of viability of sperm and unfertilized eggs. Eggs remained highly viable for only 5 min, sperm for 10 min. Spawning when current velocities were low, reduced dispersion of milt, thus increasing the likelihood of egg fertilization.

Introduction

The atlantic silverside, *Menidia menidia*, is a ubiquitous resident of East Coast estuaries from the Magdalen Islands, Quebec, Canada (Cox 1921) to northern Florida (Gosline 1948, Johnson 1975). Middaugh et al. (1981) observed schooling *M. menidia* moving into the upper intertidal zone and spawning during daytime high tides from March through July. Maximum intensity spawning runs occurred every 13 to 16 days. Middaugh (1981) suggested that the interaction of tidal and diurnal spawning synchronizers (high tide – sunrise cue)

ccepted 29.4.1982

* Contribution No. 150 of the Gulf Breeze Environmental Research Laboratory.

© 1983, Dr W. Junk Publishers, ed in The Netherlands. 0378-1909/83/0082-0097/$01.60

U.S. Government is authorized to reproduce and sell this report. Permission for further reproduction must be obtained from the copyright owner.

resulted in the observed fortnightly recurrence of maximum intensity spawning runs. However, the approximate synchrony of the high tide – sunrise cue (occurrence of a high tide <1 hour after sunrise), and new and full moons prevented determination of the relative contribution of these factors in cueing spawning.

In this paper, we present data from field and laboratory observations that describe the importance of tidal and diurnal spawning cues in *M. menidia* and discuss the potential adaptive significance of timing of spawning runs by this fish.

Experiments determined: 1) the relationship between decreased current velocities at high tide in the field and timing of spawning runs; 2) the influence of simulated decreases in tidal current velocities (at high tide) and light cycles on timing of spawning in the laboratory; and 3) the duration of viability of eggs and sperm stripped from mature adults just prior to a spawning run.

Materials and methods

Spawning in the field

Observations of the timing of spawning runs relative to decreases in current velocities at high tide were made at Bears Bluff, Wadmalaw Island (32° 38′ 42″ N lat., 80° 15′ 18″ W long.) on the North Edisto River estuary in South Carolina. The study site was described in detail by Middaugh et al. (1981).

Tidal current velocities were measured 3 m offshore from the outer edge of cordgrass, *Spartina alterniflora*. A perforated plastic golf ball that floated with its top at the air-water interface was used to measure current velocities (cm sec^{-1}).

The elapsed time for transit of the ball between two pipes, placed 1 m apart and parallel to the flow of flood and ebb tides was measured. Preliminary calibration tests showed nearly identical results for the ball (N = 9, grand $\bar{x}$ = 37.8 cm sec^{-1}, S = 8.4) and a current meter (N = 9, grand $\bar{x}$ = 38.4 cm sec^{-1}, S = 10.1).

Current velocity measurements were taken at 5 min intervals from 90 min before until 90 min after daytime high tides on 14, 15, 21, 29, 30 and 31 May, and 16 June 1980. Wind velocity on these days was <2 kts.

Spawning runs were observed on each date at Bears Bluff. The time of onset and end of spawning runs was noted as well as behavior of *M. menidia* for approximately 90 min before, during, and 90 min after a spawning run.

Tidal and diurnal spawning cues

Laboratory spawning experiments were conducted to elucidate the response of *M. menidia* to periodic decreases in tidal current velocities and diel light cycles. Fertilized eggs, stripped from ripe females on 19 March 1979 were maintained in an aerated 160 l glass aquarium at 26‰ and 22° C with a 14 h light.10 h dark (14 L:10 D) photoperiod provided by 'daylight' fluorescent lamps. Light intensity during laboratory experiments ranged from 1600 to 2000 lux. Hatching occurred on 29 March 1979; larval *M. menidia* were fed *Artemia* nauplii twice daily.

After 30 days, juvenile *M. menidia* were transferred to a recirculating culture system that consisted of two 1 m diameter fiberglas spawning tanks (water 45 cm deep), a crushed oyster shell and activated charcoal filter, and reservoir. A March *TE 5C MD pump circulated seawater from the reservoir to each spawning tank via 1.5 cm I.D. plastic pipe.

A jet of water, produced by pumping water through an 8 mm diameter hole, drilled in a pipe cap produced mean surface current velocities of 8.0 cm sec^{-1}. Water flowed out of the bottom of each tank through a jacketed standpipe. An airstone positioned at the outer bottom edge of each jacketed standpipe maintained dissolved oxygen concentrations >5 mg l^{-1}. Water temperature ranged from 16 to 25° C. Salinity was 30 ± 2‰.

Approximately 50 *M. menidia* were maintained in each spawning tank from 28 April 1979 to 20 June 1980. They were fed 8 g of Tetramin® large flake food each morning (0730 to 0930) and afternoon

* Mention of trade names does not imply endorsement by the U.S. Environmental Protection Agency or Nagasaki University.

(1330 to 1530) during the week. Approximately 6 g of live *Artemia* nauplii were added to each tank between 1000 and 1100. On weekends, *M. menidia* were fed Tetramin[R] and *Artemia* nauplii once daily at varying times.

The photoperiod was 24 L:0 D from 28 April 1979 until 22 February 1980. The seawater circulation pump ran continuously from 28 April 1979 to 10 January 1980. Between 11 January and 22 February, the circulation pump was turned off for 1 h twice daily, from 1200 to 1300 and 2400 to 0100. This circulation regime allowed determination of the influence of decreased current velocities (8.0 cm sec^{-1} to 0.0 cm sec^{-1} within 10 min of cessation of pump circulation) on spawning with constant lighting.

In order to elucidate the effect of a diel light cycle on spawning, in combination with decreased current velocities at noon and midnight, we changed the photoperiod from 24 L:0 D to 14 L:10 D on 23 February. This modified light regime provided information on the response of *M. menidia* to: 1) 'lights-on' at 0500 with a constant current velocity of 8.0 cm sec^{-1}; 2) a decrease in current velocity at noon with lights-on; and 3) a decrease in current velocity at midnight with lights-off.

A spawning substrate made of aquarium filter fiber (Longlife Aquarium Products, Harrison, N.J. 07029) approximately 15 cm long × 10 cm wide × 10 cm thick was suspended just below the water's surface in each spawning tank. Substrates were checked at 0700 and 1305 each day during the week and once daily on weekends. If embryos were found, the developmental stage was determined and time of spawning estimated from observations on developmental rates made during this study. New spawning substrates were then placed in holding tanks.

Sperm and egg viability

Experiments were conducted to determine the duration of viability of sperm and unfertilized eggs. Males and females, seined from the intertidal zone just prior to the beginning of a spawning run, were isolated in separate 60 l tanks. Prior to stripping, females were dipped in a series of three containers of clean seawater and rinsed with aged (24 h old) seawater to remove extraneous sperm which might have adhered to their bodies or have been in the water of the holding containers. Ova were stripped from 3 to 5 females into a 10 cm diameter glass culture dish that contained seawater. After stripping, approximately 50 unfertilized eggs were quickly distributed to replicate 4.0 cm diameter glass culture dishes containing 50 ml of seawater.

Sperm from 3 to 5 males was stripped into 4 cm diameter glass culture dishes that contained 50 ml of seawater. Aliquots (2 ml) of sperm, <1 min old, were added to replicate dishes of unfertilized eggs that had aged for 1.0, 2.5, 5.0, 10.0, 20.0, 40.0 and 80.0 min. Eggs were checked 24 h after addition to culture dishes to determine if fertilization had occurred. Eggs transferred to 4 cm diameter culture dishes, without subsequent addition of sperm, were maintained as fertilization controls.

A similar procedure was used to determine sperm survival. Approximately 50 eggs, <1 min old, were added to aged milt-seawater solution and checked after 24 h for fertilization. All tests were conducted at 24 to 26° C and 25‰.

Results and discussion

Tidal and diurnal spawning cues

Earlier, field observations by Middaugh (1981) showed that large numbers of *M. menidia* were present at spawning sites during nighttime high tides, but neither schooled nor spawned. At sunrise, attainment of light intensity sufficient for a visual schooling response (>0.06 ft candles; Shaw 1961) resulted in formation of prespawning schools. Spawning runs coincided with daytime high tides. We suspect that runs occurred in response to decreased current velocities at high tide since sperm entering the water during an interval of diminished tidal currents would be less susceptible to dispersion.

Furthermore, we hypothesized that the daily 0.8 h delay in the time of high tide relative to the time of sunrise, could result in the observed spawning periodicity in *M. menidia*. The size of a pre-

spawning school would increase each day along with the increase in time from sunrise to the predicted time of high tide. Daily increases in the number of fish schooling and spawning would eventually lead to a decline in the number of spawning fish during respective semilunar (14.77 day) cycles, because a progressively larger number of individuals would be spent. Unfortunately, occurrence of new and full moons at the approximate time of the coincidence of a high tide at sunrise during each semilunar period prevented determination of the relative importance of lunar and high tide-sunrise cues in synchronizing spawning runs of *M. menidia* (Middaugh 1981).

In this study, we documented the onset and end of spawning runs in response to decreased tidal currents during daytime high tides. Current velocities ranged from a high of 16 cm sec^{-1} to 3 cm sec^{-1} ($\bar{x}$ = 11 cm sec^{-1}) at the onset of spawning. Runs ended when ebb tide current velocities were between 5 and 22 cm sec^{-1}, ($\bar{x}$ = 17 cm sec^{-1}) (Fig. 1).

Behavior of pre-spawning schools of *M. menidia* just prior to spawning indicated that they probably responded to the availability of spawning substrates as well. On several occasions schooling *M. menidia* made repeated passes by an area where spawning often occurred. However, as high tide approached, the spawning substrate remained unavailable because of low tidal amplitude. Just before high tide, the school moved to another spawning site, lower in the intertidal zone, and began to spawn. The end of spawning runs may also have been influenced by inaccessibility of substrates as tidal heights decreased during ebb tide (Fig. 2 and Table 1).

Laboratory experiments demonstrated the influence of tidal and diurnal cues in spawning of *M. menidia*. Since fish in each spawning tank responded similarly, data were pooled for analysis.

A 24 L:0 D photoperiod resulted in spawning at 1200 to 1300 and 2400 to 0100 in response to decreased current velocities (Fig. 3A, B). Alteration of the photoperiod to 14 L:10 D caused spawning shortly after lights-on in the morning, 0500 to 0600, in spite of an uninterrupted current velocity of 8.0 cm sec^{-1}. In addition, spawning occurred between 1200 and 1300 in response to decreased current velocities (Fig. 4A, B). No spawning occurred during nighttime, even though current velocities decreased to 0.0 cm sec^{-1} between 2400 and 0100 (Fig. 4A, B).

These data and earlier studies (Middaugh 1981, Middaugh et al. 1981) indicate that tidal and

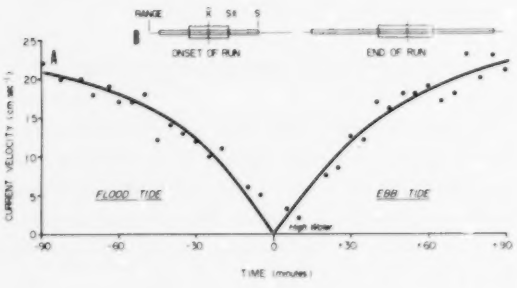

Fig. 1. A. Current velocities measured adjacent to spawning sites at Bears Bluff. *B.* range, mean ($\bar{x}$), standard error (S $\bar{x}$) and standard deviation (S) for the corresponding time of onset and end of spawning runs.

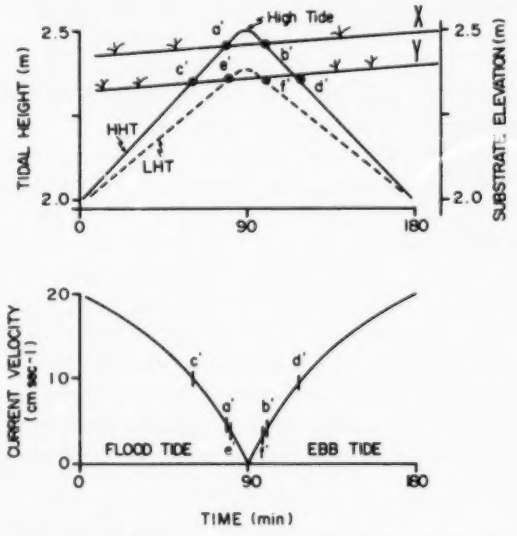

Fig. 2. Conceptual model of factors which may influence the onset and end of spawning runs in *Menidia menidia*. Tidal height from 90 min before until 90 min after high tide, HHT – higher high tide, LHT – lower high tide; the elevation of two spawning substrates (X and Y) is also shown, and (lower figure) corresponding tidal current velocities (cm sec^{-1}) measured during the present study. Lower case letters (a' – b', c' – d', e' – f') indicate intervals when respective spawning substrates would be available (inundated).

Table 1. Summary data for tidal heights and measured tidal current velocities at the onset and end of spawning runs. The corresponding time (in minutes) that spawning substrates would be available at two intertidal elevations is estimated. Locations of intertidal spawning substrates (a' – b', c' – d', e' – f') are shown in Figure 2.

Spawning substrate	Higher high tide (HHT)	Lower high tide (LHT)	Location	Onset of run current vel. (cm sec^{-1})	Location	End of run current vel. (cm sec^{-1})	Substrate available (min)
X	√	–	a'	4.5	b'	4.5	23
Y	√	–	c'	10.0	d'	10.0	56
X		*	–	–	–	–	–
Y		√	e'	3.7	f'	3.7	19

* unavailable as a spawning substrate because of low tidal height.

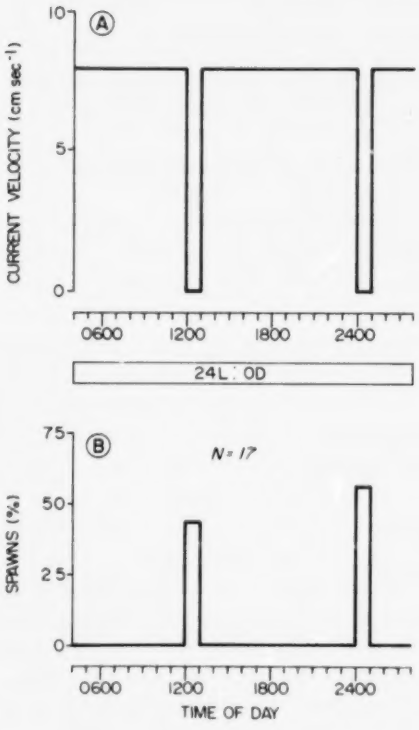

Fig. 3. A. Current velocity in spawning tanks. *B.* spawning in response to decreased current velocities at 1200 to 1300 and 2400 to 0100. Lights were on continuously 24 L:0 D.

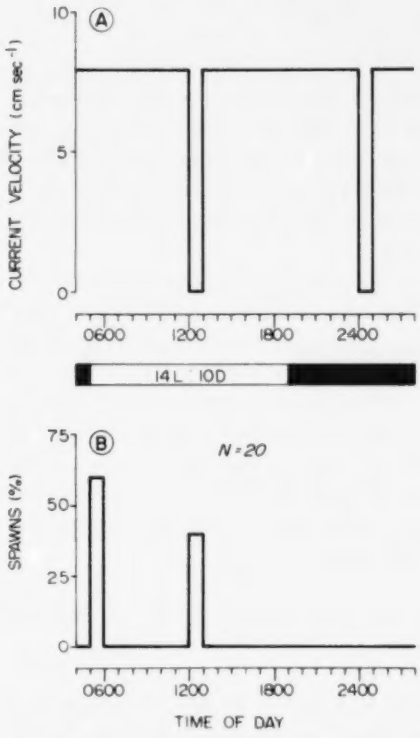

Fig. 4. A. Current velocity in spawning tanks. *B.* spawning in response to 'lights-on' at 0500 to 0600 and decrease current velocities at 1200 to 1300. No spawns occurred in response to decreased currents during darkness 2400 to 0100. Photoperiod was 14 L:10 D.

diurnal cues synchronize spawning runs of *M. menidia*. 'Lights-on' in the laboratory (in the presence of an uninterrupted current velocity of 8.0 cm sec^{-1}) could have served as a spawning cue for several reasons: 1) limited spatial dispersion of schooling fish at night assured rapid regrouping of schools each morning, followed by spawning; 2) the uninterrupted current velocity (8.0 cm sec^{-1}) was less than the mean threshold velocity (11 cm sec^{-1}) for onset of spawning in the field (Fig. 1); 3) tidal amplitude did not limit the time that spawning substrates were available in holding tanks; and 4) spawning substrates may have provided an area sheltered from current velocities, since Moore (1980) reported that *M. menidia* spawned on the sheltered (downstream) side of a floating dock during ebb tide.

Egg and sperm viability

Results of tests to determine the longevity of unfertilized eggs and sperm indicated similar responses for each. Eggs remained highly fertilizable for only 5 min. Sperm remained highly fertile for up to 10 min. Viability of unfertilized eggs and sperm decreased rapidly between 10 and 20 min after stripping (Fig. 5).

Timing of spawning runs in the intertidal zone to coincide with decreased current velocities at high tide helped to reduce dispersion of sperm. The short term viability of unfertilized eggs and sperm and infrequent pairing of spawning adults (Middaugh et al. 1981) suggest that slow dispersion of sperm is important in assuring egg fertilization. Goode (1884) also observed that *M. menidia* spawned on high tides and that water in the spawing zone was whitened with sperm.

Significance of spawning periodicities in intertidal fishes

Other studies have demonstrated spawning runs in fishes coinciding with physical variables. Benzie (1968) reported that the whitebait, *Galaxias maculatus*, spawned in vegetation in the upper intertidal zone of a New Zealand estuary during daytime high tides, and provided evidence that suggests that *G.*

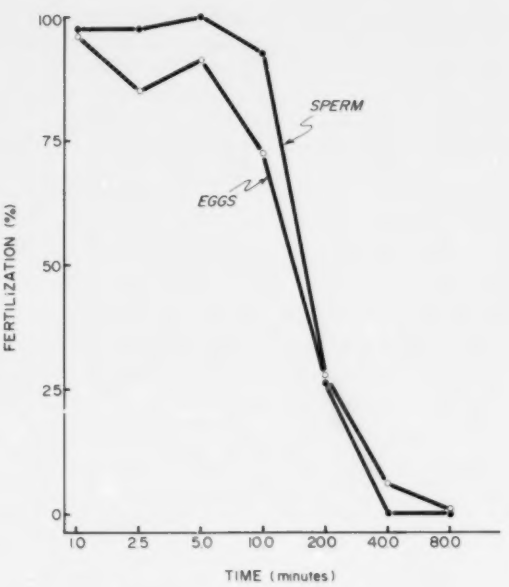

Fig. 5. Percent fertilization (viability) for eggs and sperm stripped from mature adults and aged for specified times.

maculatus may have spawned in areas isolated from strong water currents.

Similar behavior was reported for the Pacific surf smelt, *Hypomesus pretiosus*, on the Washington coast (Loosanoff 1937). Fish appeared near shore during the latter part of flood tide, swimming back and forth along the edge of the beach. Fish began spawning 1 to 1.5 h before high tide, and continued for about 1 h after high water. Spawning was always more active during afternoon flood tides, especially if the high tide coincided with sunset. Penttila (1978) observed spawning of *H. pretiosus* during evening, night and morning high tides in water a few cm deep in Puget Sound.

The California grunion, *Leuresthes tenuis*, and Gulf grunion, *L. sardina*, both time spawning runs to coincide with high tides. Clark (1925) and Walker (1949, 1952) observed that *L. tenuis* spawned on southern California beaches during nighttime every two weeks, generally on the highest high tides. Sperm from one or more attendant males, deposited on the sand in close proximity to females, flowed down their bodies and fertilized eggs. Egg deposition during a period of substrate

stability (Shepard & LaFond 1940, Middaugh et al. 1982), and reduced predation of adults and embryos probably are crucial factors in the reproductive ecology of *L. tenuis*.

Leuresthes sardina shows similar spawning behavior in the Gulf of California. However, from January to May, there is a transition from spawning on nighttime to daytime high tides. Thomson & Muench (1976) attributed the shift to a change in the occurrence of the highest high tides from early morning, 0300 to 0500, to late afternoon, 1500 to 1700. In addition, they attributed rapid spawning on the beach to the short wave period in the Gulf of California, in contrast to the longer period waves of southern California beaches where *L. tenuis* spawns.

Taylor et al. (1979), and Taylor & DiMichele (1980) reported a diel cycle in gonadal maturity and spawning readiness, superimposed on a lunar spawning rhythm in the mummichog, *Fundulus heteroclitus*. During daytime, eggs were usually dispersed throughout the stroma of the ovary. Fish sampled on nighttime high tides usually contained ovulated eggs grouped posteriorly in the lumen of the ovary, at the opening of the ovipositor. Taylor et al. (1979) and Taylor & DiMichele (1980) concluded that the rhythmicity of egg maturation and spawning on the highest tides of the lunar cycle was part of a complex adaptive mechanism that caused deposition of eggs in a location that insured their incubation in a salt marsh environment away from the influence of strong tidal currents.

In conclusion, timing of spawning runs in *M. menidia* and a number of other fishes which spawn intertidally coincide with physical variables such as decreased tidal current velocities, tidal amplitude, wave period, and substrate availability and stability. Biotic factors such as predation of spawning adults and developing embryos may also influence the time and location of spawning (Middaugh 1981).

Acknowledgements

The authors are indebted to Dr. W.P. Davis of the Environmental Protection Agency, Bears Bluff Field Station for providing living quarters during the visit of T. Takita to the United States. Dr. J.M. Dean of the Belle W. Baruch Institute assisted in coordination of the visit. Mr. I.B. Johnson and Ms. R.L. Yoakum helped with maintenance of fish in the laboratory phase of this study.

References cited

Benzie, V. 1968. Some ecological aspects of spawning behavior and early development of common whitebait, *Galaxias maculatus attenuatus* (Jenyns). Proc. N.Z. Ecol. Soc. 15: 31–39.

Clark, F.N. 1925. The life history of *Leuresthes tenuis*, an atherine fish with tide controlled spawning habits. Calif. Fish. Game Comm. Bull. 10: 1–51.

Cox, P. 1921. List of the fishes collected in 1917 off Cape Breton coast and the Magdalen Islands. Contrib. Canadian Biol. (1919–1920) 11: 109–114.

Goode, G.B. 1884. Natural history of useful aquatic animals. Pt. 3. The food fishes of the U.S. In: Fish. Ind. Res. U.S., Sec. 1, p. 457.

Gosline, W.A. 1948. Speciation in the fishes of the genus *Menidia*. Evol. 2: 306–313.

Johnson, M.S. 1975. Biochemical systematics of the atherinid genus *Menidia*. Copeia 1975: 662–691.

Loosanoff, V.L. 1937. The spawning run of the Pacfic surf smelt, *Hypomesus pretiosus* (Girard). Intern. Rev. ges. Hydrobiol. Hydrogr. 36: 170–183.

Middaugh, D.P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Copeia 1981: 766–776.

Middaugh, D.P., G.I. Scott, & J.M. Dean. 1981. Reproductive behavior of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Env. Biol. Fish. 6: 269–276.

Middaugh, D.P., H.W. Kohl III & L.E. Burnett. 1982. Concurrent measurement of intertidal environmental variables and embryo survival for the California grunion, *Leuresthes tenuis*, and Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Calif. Fish and Game. (In press).

Moore, C.J. 1980. Spawning of *Menidia menidia* (Pisces: Atherinidae). Copeia 1980: 886–887.

Penttila, D. 1978. Studies of the surf smelt (*Hypomesus pretiosus*) in Puget Sound. State of Washington, Dept. Fish., Tech. Rept. No. 42.47 pp.

Shaw, E. 1961. Minimal light intensity and the dispersal of schooling fish. Bull. Inst. Oceanogr. Monaco 1213: 1–8.

Shepard, F.P., & E.C. LaFond. 1940. Sand movements along the Scripps Institution pier. Amer. Jour. Sci. 238: 272–285.

Taylor, M.H., G.J. Leach, L. DiMichele, W.M. Levitan & W.F. Jacob. 1979. Lunar spawning cycle in the mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae). Copeia 1979: 291–297.

Taylor, M.H. & L. DiMichele. 1980. Ovarian changes during the

lunar spawning cycle of *Fundulus heteroclitus*. Copeia 1980: 118–125.

Thomson, D.A. & K.A. Muench. 1976. Influence of tides and waves on the spawning behavior of the Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann). Southern Calif. Acad. Sci. Bull. 75: 198–203.

Walker, B.W. 1949. Periodicity of spawning by the grunion, *Leuresthes tenuis*, an atherine fish. Ph.D. Dissertation, University of California, Los Angeles. 166 pp.

Walker, B.W. 1952. A guide to the grunion. Calif. Fish and Game 38: 409–420.